A Review of the Pathogens and Parasites
of the Biting Midges (Diptera: Ceratopogonidae)

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ABSTRACT

A review is presented of all published information on parasites and pathogens of biting midges of the dipterous family Ceratopogonidae. Viruses furnished two records; Rickettsiae 1; Bacteria 6; Fungi 8; Protozoa 23; Nematoda 21; Acarina 18; and Insecta Hymenoptera 4. A bibliography of 90 titles is given. It is believed that mermithid nematode parasites offer some promise in biological control of *Culicoides* disease vectors.

The literature on natural enemies of biting midges is not extensive. Helpful reviews were published by Weiser (1963a, 1975), Jenkins (1964), and Bacon (1970). This review has been prompted by my involvement in 3 related review projects: 1) a compilation of a complete bibliography and a key-word in-context index to the published literature on the Ceratopogonidae (Atchley, Wirth, and Gaskins, 1975); 2) preparation of introductory chapters on ceratopogonid biology for a manual to the genera of the Ceratopogonidae (Wirth, Ratanaworabhan, and Blanton, in preparation); and 3) preparation of a chapter on parasites and pathogens of biting midges for a revision of Jenkins' World Health Organization bulletin (1964). In each of these activities different emphasis has been placed on content and organization of the information to be included, depending on the primary purpose of the review. I am here choosing a format to bring to the attention of workers interested in the control of biting midges a resumé of the known pathogens and parasites offering the most promise in biological control.

For brevity a decision was made, perhaps too arbitrarily, to exclude, or to mention only briefly, references to several groups of parasites of ceratopogonids that probably would have little significance in biological control. These include protozoan and nematode parasites pathogenic to birds and mammals for which ceratopogonids are known to be alternate hosts without suffering known adverse effects from the parasitism. Examples are bluetongue virus and the filarial parasites just mentioned, and *Haemoproteus*, *Hepatocystis*, and *Leucocytozoon* protozoans. Some of these organisms have considerable medical or veterinary literature concerned with disease transmission in vertebrate hosts.

A discussion of predators of Ceratopogonidae would be too long and involved to include here and should be the subject of a separate review. The prey habits of predators tend to be less specific, and preliminary studies of predation tend to

include more fortuitous records than studies of parasites and pathogens. Our interest and knowledge of the possibilities of biological control of biting midges are still in such an early stage that a meaningful review cannot be made. Yaseen (1974) searched for natural enemies of West Indian ceratopogonids for nearly a year without finding any parasites or pathogens. The only natural enemies found were adults of a tiger-beetle, *Cicindela suturalis* F., which fed on pupae and adults of *Culicoides phlebotomus* (Williston).

Insect resistance to pesticides and environmental concerns about long-range effects of repeated applications of pesticides have led to emphasis on alternative methods of control. Integrated control, which calls for the timely and frugal application of pesticides while exploiting every possibility for the use of natural enemies and habitat management, offers the maximum promise for relief from damage and annoyance caused by insect problems. A detailed knowledge of the ecology of insect pests and their natural enemies is essential for effective control.

Compared with mosquitoes, lice, fleas, and some other bloodsucking pests of man and domestic animals, research on the biology and natural enemies of biting midges (Ceratopogonidae) has received little emphasis. Because of their small size and difficulty of colonization comparatively little work has been done in determining ceratopogonid vectors of disease organisms of medical and veterinary importance. Lacking a proven basis as disease vectors, the study of ceratopogonids has been further neglected. Our knowledge of natural enemies of biting midges is in an early embryonic stage, compared with what is known, for instance, for mosquitoes.

Viruses

Chapman et al. (1968) and Chapman (1973) reported the first pathogenic virus in a biting midge. Over an 11-month period in Louisiana they found nearly 50% of the larvae of *Culicoides arboricola*

Root and Hoffman from 3 tree holes infected with an iridescent virus (CuIV). Infection caused death of the larvae. Infected dead larvae placed in several other tree holes eventually produced some infected *Culicoides* larvae.

Clark and O'Grady (1975) collected larvae of *Culicoides cavaticus* Wirth and Jones from tree holes in California that exhibited symptoms of a disease similar to that caused by the "tetragonal virus" reported by Kellen et al. (1963), Clark and Chapman (1969), and Stoltz et al. (1974) in mosquitoes in California and Louisiana. "Infected larvae were easily identified by their sluggish activity, which contrasted sharply with their normally rapid swimming movements. As the disease progressed, the body of the larva stiffened, first in the middle segments and then toward both extremities. Heart pulsations could be detected after the extremities ceased movement. After death, the body remained rigid and straight until post-mortem changes resulted in the dissolution of larval tissues . . . . In the original collection, all of the *Culicoides* larvae eventually died with the symptoms just described. In subsequent collections, the mortality rate ranged from about 70 to 90%". Nonoccluded viruslike particles from various tissues of the larvae were observed with the aid of an electron microscope. Apparently normal larvae usually died about 3 days after exposure to water contaminated with the remains of larvae killed by the disease. Attempts to infect *Culex* and *Aedes* mosquito larvae and *Musca domestica* larvae by feeding them infected *Culicoides* tissues were negative.

Rickettsiae

Hertig and Wolbach (1924) found tiny, rickettsia-like cocci, diplococci, and short rods in smears of the bodies of adults of *Culicoides sanguisuga* (Coquillett) from Massachusetts. Nine out of 27 individuals were infected, the rickettsiae occurring free in smears of the abdomen, although greater numbers were seen in lobes of the fat body.
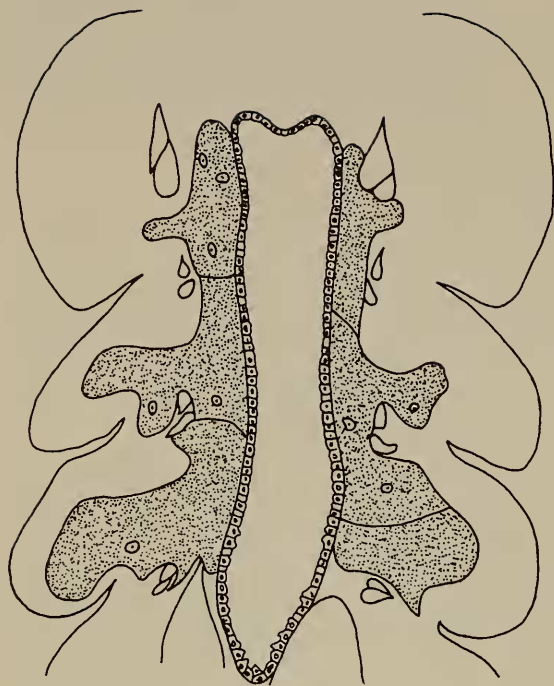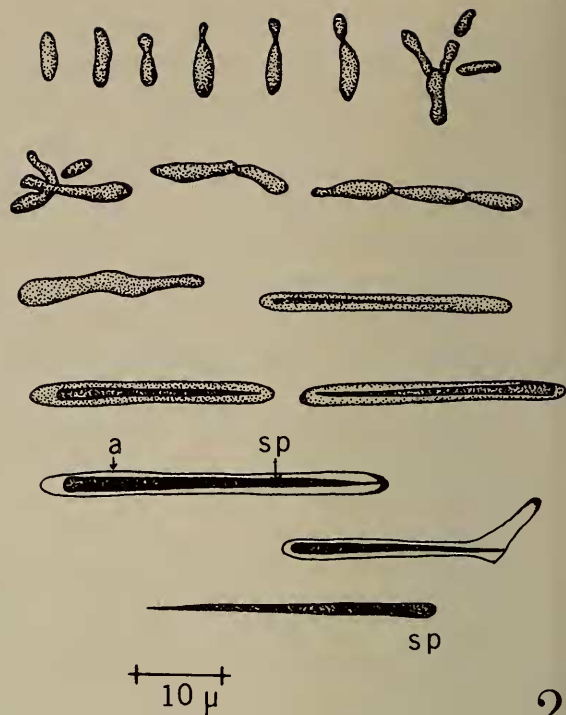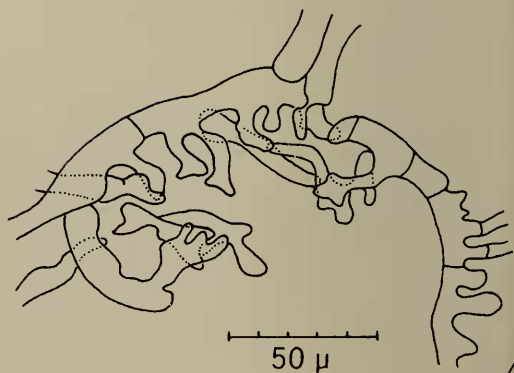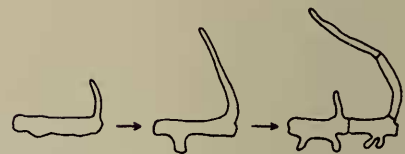
Fig. 1. Mycetome of bacteria in thorax and anterior abdominal segments of *Dasyhelea* imago (after Buchner, 1930). Fig. 2. Stages in budding cells and spore formation of the fungus *Monosporella unicuspidata* in *Dasyhelea obscura* (after Keilin, 1920); a, ascus; sp, ascospore. Fig. 3. Different aspects of the diaspores of *Carouxella scalaris* in *Dasyhelea lithotelmatica* after their liberation, showing the stout protoconidia and slender conidia (after Manier et al., 1961). Fig. 4. Adherent mycelium of *Rubettella inopinata* in *Dasyhelea lithotelmatica* (after Manier et al., 1961).

Bacteria

Keilin (1921a, 1927) found 2 pairs of masses of bacteria present in the body cavity of the thorax of *Dasyhelea obscura* (Winnertz) in England. These organisms, which he termed "hereditary bacterian symbionts," pass from stage to stage in these masses and appear in the egg stage. Stammer (in Buchner, 1930) reported similar bacteria forming a syncytium in mycetomes in the thorax of *Dasyhelea versicolor* (Winnertz) in Germany (fig. 1). Mayer (1934) observed similar mycetomes in larvae of *Culicoides* species in Germany. Lawson (1951) found bi-refringent, non-fluorescent, minute, motile particles in cells of the fat bodies of *Culicoides nubeculosus* (Meigen) in Britain, that he speculated may be symbionts of the type found by Keilin. Becker (1958) identified as *Pseudomonas* sp. fluorescent bacteria isolated from larvae of *Culicoides salinarius* Kieffer in Scotland. He presumed that these bacteria were also symbiotic.

Fungi

Keilin (1920a, 1921a, 1927) described an Ascomycete fungus, *Monosporella unicuspidata*, from the body cavity of larvae of *Dasyhelea obscura* (Winnertz) in England (fig. 2). Infected larvae could be recognized by their milky appearance. The fungus is pathogenic to the larvae, which die with the body cavity completely filled with the spores of the fungus.

Ciferri (1929) grew cultures of *Grubyella ochoterenai*, a fungus parasite originally collected in Mexico from dead bodies of *Simulium* larvae, in the laboratory in the Dominican Republic on adults of *Culicoides phlebotomus* (Williston). Mayer (1934) reported finding Ascomycete fungi of the group Laboulbeniales on *Forcipomyia* sp. in Germany. According to Steinhaus (1949) these fungi are usually harmless commensals.

Manier et al. (1961) described 2 new Trichomycete fungi from *Dasyhelea lithotelmatica* Strenzke in France: *Rubetella inopinata* (fig. 4) and *Carouxella*

scalaris (fig. 3). The first develops in the anterior part of the hind gut and the second in the rectal ampullae of the *Dasyhelea* larvae. Gol'berg (1969) reported an epizootic among ceratopogonid midges in a water reservoir in the filtration fields of a village near Moscow caused by *Entomophthora ovispora* Nowak.

Megahed (1956) found "fungal hyphae" in the lumen of the oesophageal diverticulum of *Culicoides nubeculosus* (Meigen) in laboratory colonies in Britain and speculated that the spores must have been ingested with raisin sap and have developed within the diverticulum. Lewis (1958) found fungal hyphae in the duct of the crop of a dissected female of *Culicoides furens* (Poey) in Jamaica.

Protozoa

Weiser (1963a) stated that while members of every protozoan class parasitize insects, the important pathogens belong to the Gregarina, Coccidia, Microsporidia, and Haplosporidia. Most species found in the intestinal tract are harmless commensals, whereas those living in the gut walls may cause tissue destruction and death of the host.

Ciliata

Ghosh (1925) described a ciliate, *Balantidium knowlesii* (fig. 5), from the coelomic cavity of *Culicoides peregrinus* Kieffer (stage not given) in India. According to Jenkins (1964) this species is a synonym of *Tetrahymena pyriformis* (Ehrenberg). Laird (1960) stated that *Tetrahymena* ciliates are normally free-living but may invade wounded or moribund larvae of mosquitoes, and sometimes even healthy ones. In 1959 Laird reported that *T. pyriformis* is a well-known facultative parasite of various mosquitoes and other aquatic insects. Chapman et al. (1969) reported a ciliate identified as *Tetrahymena* sp. from larvae of *Culicoides* probably *nanus* Root and Hoffman in Louisiana. Sharp (1928) reported unidentified ciliates from the dissected bodies of 3 out of 540
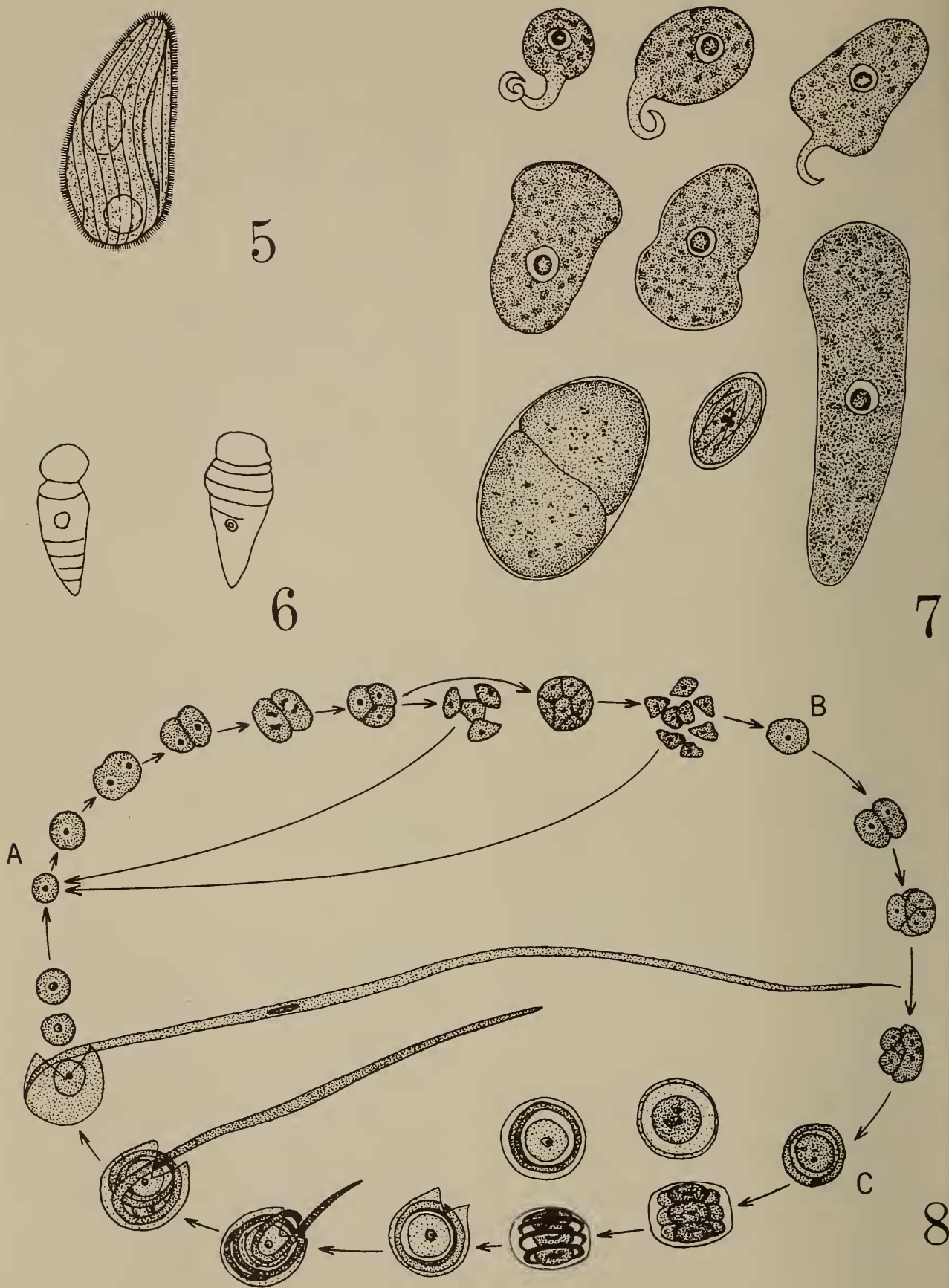
Fig. 5. *Balantidium knowlesii* from the coelomic cavity of *Culicoides peregrinus* (after Ghosh, 1925).
Fig. 6. *Taeniocystis parva*, a gregarine from the larva of *Forcipomyia* sp. (after Foerster, 1938). Fig. 7.
Stylocystis riouxi, an eugregarine parasite from the larva of *Dasyhelea lithotelmatica* (after Tuzet and
Ormières, 1964). Fig. 8. Life cycle of *Helicosporidium parasiticum* from *Dasyhelea obscura*; a,
schizogonic multiplication; b, formation of morula; c, spore formation; d, stages in opening of
sporocyst, unrolling of spiral filament, and liberation of sporozoite (after Keilin, 1921).

wild-caught females of *Culicoides austeni* Carter, Ingram, and Macfie in the Cameroons.

Becker (1958) reported ciliates identified as *Perezella* sp. (Perezellidae, Astomata) living in the haemocoeles of *Culicoides* larvae in Scotland. Up to 20% of the larvae in various samples were parasitized, and the number of parasites per larva varied from a few until they became closely packed in the haemocoel. *Culicoides salinarius* Kieffer, *odibilis* Austen, and *riethi* Kieffer were parasitized. Becker quoted unpublished observations of Kettle in Scotland of these parasites in a larva of *C. pulicaris* (L.), and of ectoparasitic cysts, presumably also of *Perezella*, occurring frequently near Glasgow on larvae of *C. cubitalis* Edwards and *pallidicornis* Kieffer. Kettle and Lawson (1952, plate 17a) illustrated these "ectoparasites" on the head and neck of a *C. pallidicornis* larva.

Mastigophora

Weiser (1963a) believes that gut flagellates found in the intestinal tract of insects are harmless commensals. Sharp (1928) reported, for example, that flagellates of the leptomonas type were seen on a number of occasions in dissections of females of *Culicoides austeni* Carter, Ingram, and Macfie in the Cameroons. Kremer et al. (1961) observed that a large proportion of the larvae of *Culicoides salinarius* Kieffer had in their digestive tube a small flagellate similar to but smaller than the *Strigomonas* found in *Culex*.

Recently Hommel and Croft (1975) discovered a flagellate which they placed in the genus *Herpetomonas* Kent infecting 2 to 5% of the adults in the laboratory colony of *Culicoides variipennis* (Coquillett) at Pirbright, England. The parasites were always localized in the Malpighian tubules and sometimes in the midgut and hindgut of the adult midges, and occurred in either opisthomastigote or promastigote stages with a long flagellum. In culture on 4N medium the parasites transformed into aflagellar multiplicative stages with a high degree of polymorphism. The forms with long flagella reappeared in culture after 6 to 8 days. The life cycle was not worked out, but the authors believed that probably early stage midge larvae were infected by forms released by the adult midges. This was the first record of a *Herpetomonas* in the family Ceratopogonidae.

Gregarinida

According to Weiser (1963b) the gregarines parasitic in insects fall in two main classes: (1) Eugregarina, most of which are harmless gut-inhabiting commensals, rarely invading the epithelial tissues, and have lost the schizogonous part of their life cycle. (2) Neogregarina (or Schizogregarina) which invade and undergo schizogony in the gut wall or other tissues and often cause death or serious harm to their host. Tuzet and Rioux (1965) reviewed the classification and life cycles of the gregarines of Ceratopogonidae and other biting Nematocera including the species discussed below.

Schizocystis gregarinoides Léger (1900) is a neogregarine parasite in the gut wall of *Ceratopogon* sp. (Léger, 1900) and *Bezzia solstitialis* (Winnertz) (Léger, 1906) in Europe, parasitizing up to 50% of the larvae sampled and causing the death of the host during metamorphosis. On the other hand the eugregarine *Taeniocystis mira* which Léger (1906) described from *B. solstitialis* in France is less common, infecting up to 20% of the larvae observed, with only 1 to 4 parasites in each larva, and causing little pathological damage to its host. Foerster (1938) described a second *Taeniocystis* species, *T. parva* (fig. 6), from larvae of *Forcipomyia* sp. in Germany.

Keilin (1920b, 1927) described an eugregarine, *Allantocystis dasyhelei*, from larvae of *Dasyhelea obscura* (Winnertz), which lives in decomposed sap in wounds of trees in England. These parasites were rare, and the hosts were never heavily infected; all stages of the gregarine live in the midgut of the insect larva between the intestinal epithelium and the peritrophic tube. A fourth

eugregarine ceratopogonid parasite, *Stylocystis riouxi* (fig. 7), was described by Tuzet and Ormières (1964) from larvae of *Dasyhelea lithotelmatica* Strenzke in France.

Microsporidia

According to Weiser (1963a) the Microsporidia are the commonest parasites of medically important insects. Infected hosts are not easily detected unless their bodies are transparent enough to distinguish the opaque-white tissues packed with masses of spores. Microsporidia are pathogenic to some insects while having little pathogenicity to others, having reached a suitable equilibrium with their host.

Léger and Hesse (1922) described 2 microsporidians from the fat bodies of the larvae of *Ceratopogon* sp. in France: *Spironema octospora* and *Toxonema vibrio*. According to Jírovec (1937) and Weiser (1963b) the correct names for these parasites are now *Spiroglugea octospora* (Léger and Hesse) and *Toxoglugea vibrio* (Léger and Hesse). Keilin (1927) also mentioned a parasite which he stated was probably a *Glugea* sp., invading the fat body and salivary glands of *Dasyhelea* larvae in England.

Weiser (1957, 1961, 1963b) described *Nosema sphaeromiadis* from a larva of *Sphaeromias* sp. in Czechoslovakia. The parasites were found in the fat body of the larva. Chapman et al. (1967, 1968, 1969) reported 2 species of *Plistophora* (also nosematids) from at least 2 species of *Culicoides* in Louisiana. One species was observed in *Culicoides* larvae from a shaded woodland pool. A second species in larvae of *Culicoides nanus* Root and Hoffman from tree holes caused death just before pupation. In 1969 *Plistophora* sp. was found in *Culicoides arboricola* Root and Hoffman. Chapman (1973) later reported another parasite of *C. nanus*, an unnamed new species of *Nosema*, from another tree hole at his laboratory. He stated that the levels of infection in these field populations were always less than 1% and that attempts to transmit these parasites to mosquitoes were unsuccessful.

Helicosporidia

Some workers consider this group is closely related to the Microsporidia, but with a peculiar sporogony in which the sporoblast (fig. 8) divides into 4 cells included in a spherical spore. Three of these cells develop into sporozoites, but the fourth changes into a long nucleated filament which apparently functions in opening the spore like an uncoiling spring. The only named species is *Helicosporidium parasiticum* Keilin (1921a), described from larvae of *Dasyhelea obscura* (Winnertz) in England. Later this parasite was reported from a wide range of insect hosts in Europe and North and South America (Weiser, 1970; Kellen and Lindegren, 1973). Weiser considered *Helicosporidium* more likely to be a primitive Ascomycete fungus related to the Nematosporoideae of the Saccharomycetaeae, but Lindegren and Hoffman (1976) suggested that the spore structure showed more affinity with the Protozoa than with the Ascomycete fungi. Most recently Fukuda et al. (1976) were of the opinion that the *Helicosporidium* infecting beetles and mosquitoes were 2 distinct species differing from *H. parasiticum*. They indicated that these parasites showed considerable promise as biological control agents against mosquitoes, but that this is dependent upon further testing for safety to mammals and other non-target organisms.

Haemosporidia

Several Haemosporidia are found in ceratopogonid adults but will only be mentioned briefly here because of their minor pathogenicity to the insect hosts. Their primary interest as parasites concerns their pathogenicity to their vertebrate hosts. Fallis and Bennett (1961) and Bennett et al. (1965) have reviewed this group, which includes such genera as *Parahaemoproteus* which undergoes part of its life cycle in various birds and

part in *Culicoides* midges; *Akiba caulleryi* (Mathis and Léger), a pathogenic parasite of poultry in Japan transmitted by *Culicoides arakawai* (Arakawa); and *Hepatocystis kochi* (Laveran), a malaria parasite of *Cercopithecus* monkeys in Kenya transmitted by *Culicoides adersi* Ingram and Macfie.

Nematodes

The nematode parasites of biting midges offering the most promise in biological control belong in the superfamily Mermithoidea, family Mermithidae (Nickle, 1972, 1973). However, mention should be made of several filarial parasites of vertebrates that use Ceratopogonidae as their alternate hosts.

Filarioidea

Many important mosquito-borne filarial parasites of man and domestic animals are well known, for example *Wuchereria bancrofti* (Cobbold) causing elephantiasis in man over much of the tropics, and *Dirofilaria immitis* (Leidy) causing heatworm of dogs and cats. *Onchocerca volvulus* (Leuckart), causing blindness in man in Africa and Central America, is transmitted by Simuliidae. It has been shown that *Dirofilaria* infections may produce heavy mortalities in *Aedes aegypti* (Linnaeus) vectors and that *Simulium* mortality increases with heavy infections of *O. volvulus*. It could also be expected that ceratopogonids, being much smaller insects than mosquitoes or blackflies, would suffer heavy mortality from filarial parasitism. Schacher (1973) gave a comprehensive review of filarial life-cycle patterns and a synopsis of life cycles including insect vectors.

Acanthocheilonema perstans Manson, a non-pathogenic parasite of man in Africa, is transmitted by several *Culicoides* species, notably *C. austeni* Carter, Ingram, and Macfie, and *C. inornatipennis* Carter, Ingram, and Macfie (Sharp, 1928; Hopkins and Nicholas, 1952; Duke, 1954, 1956). Another human filaria in Africa, *Dipetalonema strepto-*cerca Macfie and Corson, is transmitted by *Culicoides grahamii* Austen (Henrard and Peel, 1949; Duke, 1954). A non-pathogenic human filaria, *Mansonella ozzardi* Manson, was found to be transmitted by *Culicoides furens* (Poey) by Buckley (1934) in the West Indies, and Romaña and Wygodzinsky (1950) infected *C. paraensis* (Goeldi) with this parasite in Argentina.

Filarias of the genus *Onchocerca* are transmitted by *Culicoides* species as well as by blackflies. Steward (1933) infected *C. obsoletus* (Meigen) and *C. nubeculosus* (Meigen) with *Onchocerca reticulata* Diesing, the filaria that causes fistulous withers in horses in Europe and North America.

Bergner and Jachowski (1968) traced the development of *Macacanema formosana* Schad and Anderson, a filarial parasite of Taiwan monkeys, in *Culicoides amamiensis* Tokunaga in Taiwan. Robinson (1961) reported early development of microfilaria in *Culicoides crepuscularis* Malloch that had fed on an infected starling, and in 1971 found that *C. crepuscularis* was the vector of *Chandlerella quiscali* (von Linstow), a filarial parasite of grackles. *Forcipomyia* (*Lasiohelea*) *velox* (Winnertz) was found by Desportes (1941, 1942) to transmit a filarial worm *Icosiella neglecta* Diesing, in frogs in France.

Mermithoidea

According to reviews by Welch (1963), Bacon (1970), and Nickle (1972, 1973) most of the mermithoid parasites of Ceratopogonidae fall in the family Mermithidae. In this family only the larval stages of the worm are found in the body of the insect host. In a typical life cycle of Mermithidae the second stage juvenile nematode, armed with an odontostyle, penetrates the host cuticle and enters the haemocoel. The mermithid feeds on the haemolymph, grows, molts through a number of larval stages, and when approaching maturity, exits through the host cuticle. Mermithids usually select an early instar larva to parasitize;

those that parasitize aquatic insects may be host specific or have a wide range of related host species.

There are 2 types of life cycles in aquatic mermithids. In the first, illustrated by the mosquito parasite, *Romanomermis culicivorax* Ross and Smith, the mermithid eggs are laid in the bottom of a mosquito pool. After hatching the mermithid larva penetrates an early instar mosquito larva, often migrating to the thorax, grows quickly, and emerges from the fourth instar mosquito larva which is killed before pupation. Within 2 or 3 weeks the nematode molts, mates, and lays up to 3000 eggs in the bottom of the pool. This type of mermithid life cycle offers great promise in biological control, and the laboratory culture and release of mermithid eggs is now being undertaken on a large scale over the world. The *Romanomermis* parasite of *Culicoides nanus* Root and Hoffman reported by Chapman et al. (1968) and Chapman (1973) has this type of life cycle (Chapman, pers. com.).

In the second type of life cycle, illustrated by *Perutilimermis culicis* (Stiles) from the saltmarsh mosquito, the mermithid eggs are also laid in the bottom of a mosquito pool. The mermithid larva hatches and enters an early instar mosquito larva, remaining in the head of thorax and not growing at this time. When the mosquito pupates, the mermithid moves to the abdomen but does not enlarge until the mosquito reaches the adult stage and after it has had a blood meal. The mermithid grows rapidly and sterilizes the mosquito, then leaves the host, killing it in the process, while still a larva. The mermithid then enters the pond, molts, mates, and lays thousands of eggs to complete the cycle. Probably most mermithid parasites of aquatic ceratopogonids will have this type of life cycle, although none has yet been worked out in biting midges.

Most of the records of mermithid parasitism in ceratopogonids have to do with the formation of intersexes. In chironomids, which have been investigated in detail, Wülker (1961) found that both sexes were equally parasitized by mermithids and that intersexes had the same cytological sex chromosomes as the sex indicated by their external genitalia. The physiological nature of intersex formation remains poorly understood and urgently needs investigation. Apparently parasite damage to the hormonal system is the most important factor in intersex formation, and anatomic damage and metabolic disturbance are secondary.

In the family Tetradonematidae the adult stages of the worm are also found in the body cavity of the insect host (figs. 9–13). In *Aproctonema chapmani* Nickle (1969), described from *Culicoides arboricola* Root and Hoffman from Louisiana, the nematode passes through its larval stages in the host larvae, which breed in water-filled tree holes. Late instar *Culicoides* larvae may have 1 or more male and female adult worms nearly filling their body cavity. After mating the male nematode dies, and the female, filled with eggs, exits from the midge larva, causing its death. The nematode eggs are laid in the tree hole, and after hatching the infective nematode larvae parasitize other sand fly larvae.

Rubzov (1971, 1972) described a very unusual mermithid from larvae of *Culicoides nubeculosus* (Meigen) and *C. stigma* (Meigen) in Siberian U.S.S.R. as *Heleidomermis vivipara*. Apparently after the adults mate the eggs of this parasite develop within the female worm which remains within the host larva, and the hatched mermithid larvae escape directly from the dead *Culicoides* into the habitat. Further comment on the life cycle must await translation of the original reports in Russian. Additional study of this mermithid is very badly needed to determine its potential usefulness in biological control of *Culicoides variipennis* (Coquillett), the vector of the virus bluetongue disease of sheep and cattle in North America. These *Culicoides* are all closely related, falling within the subgenus *Monoculicoides*, and *C. variipennis* is likely to be susceptible to infection with this nematode. Chemical control of *C. variipennis* associated with
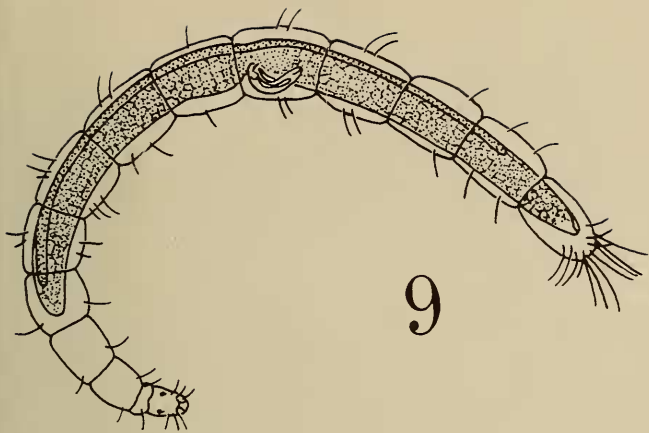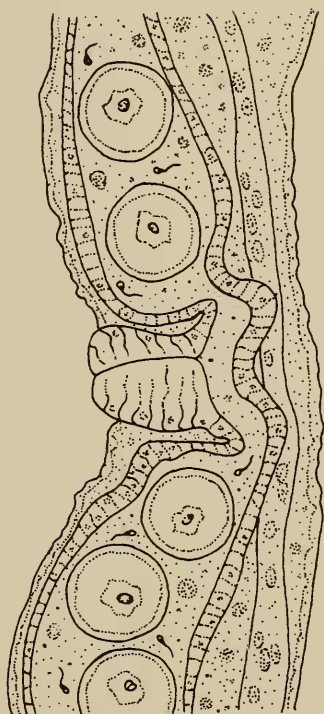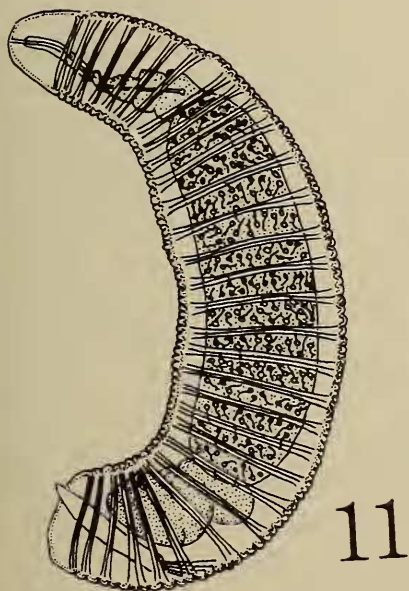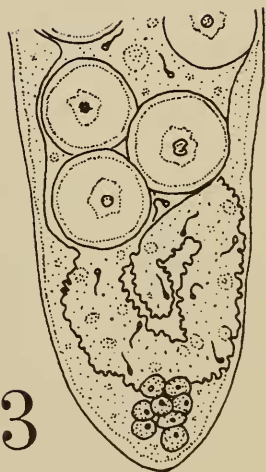
Figs. 9–13. *Aproctonema chapmani* from *Culicoides arboricola*: 9, parasitized *Culicoides* larva containing a large female and small male nematode; 10, female nematode, anterior end; 11, male nematode; 12, female nematode, vulval area; 13, female nematode, posterior end (from Nickle, 1969).

livestock has been impossible because the larvae usually breed in water-filled hoofprints and the margins of ponds or watering places contaminated with feces of the animals. Because the animals use this water for drinking, larvicides pose a toxicity problem, and some form of management or biological control is urgently needed. Control of the disease is presently based on expensive and inconvenient immunization measures.

In 1974 Rubzov described 4 additional new mermithid species from ceratopogonid larvae in the USSR: *Agamomermis gluchovae*, *Gastromermis bezzii*, *Spiculimermis mirzajevae*, and *Heleidomermis ovipara*. In contrast to *H. vivipara*, the female worm of *H. ovipara*, which develops in older instars of the *Culicoides* host larvae, is oviparous. In some populations 60% of the host larvae are infected with *H. ovipara*.

Except for the species mentioned above, very few mermithid parasites of ceratopogonids have been identified to genus, to say nothing of species. It should be noted that *Agamomermis* is an eclectic genus serving as a repository for species described from immature stages, since the generic classification is dependent on characters of the adult worm. Rubzov (1967) described *Agamomermis heleis* from an adult *Culicoides pulicaris* (L.) in the Kazakhstan SSR. Callot (1959) described an intersex adult of *Culicoides albicans* (Winnertz) in France caused by parasitism by an *Agamomermis* sp. Sen and Das Gupta (1964) reported an intersex of *Culicoides alatus* Sen and Das Gupta in India caused by *Mermis* sp., and Das Gupta (1964) reported a *Mermis* sp. causing an intersex in *Atrichopogon* sp. Parasitism of ceratopogonid adults by undetermined mermithids has been reported also by Kieffer (1914) in *Forcipomyia*, by Keilin (1921a) in *Dasyhelea*, by Whitsel (1965) and Glukhova (1967) in *Leptoconops*, and by Buckley (1938), Beck (1958), Smith (1966), Smith and Perry (1967), Glukhova (1967), Chapman et al. (1968), Boorman and Goddard (1970), Mirzaeva (1971), and Service (1974) in *Culicoides*.

In view of their conspicuous pink or reddish color and their common occurrence on adult ceratopogonids, it is surprising that so few published records exist of the association of mites with biting midges.

Trombidiiformes

Becker (1958) reported larval trombidiid mites, which were described by Vercammen-Grandjean (1957) as *Evansiella culicoides*, parasitizing adults of 4 species of *Culicoides* in Scotland. He also found larvae of another species identified as *Allothrombium* on the abdomen of a female *Culicoides heliophilus* Edwards. According to Vercammen-Grandjean and Feider (1973), *Evansiella* Vercammen-Grandjean is a synonym of *Centrotrombidium* Kramer and the correct name of the *Culicoides* parasite is *Centrotrombidium culicoides* (V.-G.). Vercammen-Grandjean and Cochrane (1974) described 3 new species of trombidiiform mites parasitizing adults of 10 *Culicoides* species in New York: *Atractothrombium dictyostracum*, *Centrotrombidium dichotomicoxala*, and *Feiderium culicoidium*. Whitsel and Schoeppner (1967) reported another trombidiid mite belonging to the genus *Valgothrombium* parasitizing a male of *Dasyhelea mutabilis* (Coquillett) in California, and quoted another report of this genus on a species of *Culicoides*. These authors quote correspondence with I. M. Newell to the effect that the mites frequent moist situations where they crawl over the substrate in search of prey. Presumably the mites locate the ceratopogonid pupae and attach themselves to the adult as soon as it emerges from the pupa. Mites have also been recorded parasitizing 4 species of "Ceratopogon" in the Sunda Islands by Salm (1914), *Culicoides austeni* Carter, Ingram and Macfie in Africa by Sharp (1928), a species of *Dasyhelea* in Argentina by Cavalieri (1968), and *Leptoconops kerteszi* Kieffer in California by Foulk (1969).

In her account of the biology of *Forcipomyia inornatipennis* (Austen) in

Ghana, Kaufmann (1974) described attacks by mites on pupae of the ceratopogonid. She stated, "The ever-present red mites do not normally attack moving prey but do so when movement ceases." Pupae attacked by mites frequently twisted themselves out of their larval exuviae fastened to the substrate and in so doing lost their fastening, and the adults were unable to emerge.

Parasitiformes

Grogan and Navai (1975) reported adult mites of the genus *Amblyseius* (family Phytoseiidae) attached to females of *Culicoides schultzei* (Enderlein) from Nepal. Grogan (1977) recorded a second adult parasitiform mite, *Macrocheles insignitus* Berlese (family Macrochelidae) parasitizing an adult female of *Nilobezzia schwarzii* (Coquillett) in Maryland.

Hydracarina

Smith and Oliver (1976) reviewed the parasitic associations of water mites with imaginal aquatic insects, and summarized the known records of Hydracarina from ceratopogonids. The typical life history pattern is as follows: The adult female mite deposits her eggs on the substrate in the aquatic habitat. Within several days the active hexapod larva hatches and seeks a suitable insect host on the surface film, in the water, or on the substrate. In any case the mite larva attaches to the adult insect at the water surface or when it emerges from the pupa at ecdysis. The mite engorges on haemolymph from the host and remains attached until the host returns to the water. With short-lived dipterous hosts, the engorged mite larva then detaches from the host, re-enters the water and seeks a place to attach its chelicerae, form a nymphochrysalis, and emerge as an active octopod nymph closely resembling the adult mite. After a variable period of maturation the nymph attaches its chelicerae to the substrate, forms an imagochrysalis and transforms to a sexually mature adult. After mating the male mites soon die but the females go on to oviposition, completing the cycle.

Munchberg (1934) reported *Hydro-droma descipiens* (Müller) parasitizing *Mallochohelea inermis* (Kieffer), apparently the first record of a water mite on ceratopogonids. Grogan and Navai (1975) reported larval aquatic mites of the genus *Tyrellia* (family Limnesiidae) parasitizing species of *Atrichopogon*, *Bezzia*, *Culicoides*, and *Dasyhelea* in Maryland. Smith and Oliver (1976) reported larvae of limnesiid mites, probably of a species of *Tyrellia*, parasitizing *Dasyhelea* in Canada. The same authors reported larval mites of the genus *Arrenurus* (family Arrenuridae) on adults of *Bezzia* and *Sphaeromias* in Canada.

Insects

Only 4 species of insects parasitic on ceratopogonids have been recorded, all in 2 closely related families of parasitic Hymenoptera, and all parasitic on the immature stages of the terrestrial and semi-aquatic genus *Forcipomyia*:

Family Diapriidae: *Entomacis longii* (Ashmead) on *F. wheeleri* (Long) in Texas (Long, 1902), and *E. californica* (Ashmead) on *Forcipomyia* sp. in Washington (Bedard, 1938).

Family Encyrtidae: *Forcipestricis gazeaui* Burks on *F. picea* (Winnertz) in Maryland (Burks, 1968; Wirth, 1975), and *F. portoricensis* Gordh on *F. fuliginosa* (Meigen) in Puerto Rico (Gordh, 1975). Apparently these parasites develop in the larvae of *Forcipomyia* and emerge from the larva or pupa, killing the host.

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